

# Dynamic variability in thermal-germination response of squirreltail (*Elymus elymoides* and *Elymus multisetus*)

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## Abstract

Bottlebrush squirreltail (*Elymus elymoides*) and big squirreltail (*Elymus multisetus*) have been identified as high-priority species for restoration and rehabilitation of millions of acres of rangeland in the western United States that have been degraded by wildfire and introduced annual weeds. In this study, squirreltail accessions from Idaho, Colorado, Utah, Arizona and New Mexico were grown in a nursery environment to produce seeds in two different years for germination evaluation at 11 constant temperatures. A statistical-gridding model was used to predict cumulative germination rate of each seedlot for eight simulated planting dates between 1 January and 28 May over a 38-year seedbed-microclimatic simulation. Predicted germination response under simulated conditions of field-variable temperatures yielded a broader ecological basis for the relative ranking of thermal response than was obtained from single-value germination indices derived from either constant-temperature experiments, or from analysis of thermal-time coefficients.

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**Keywords:** Squirreltail; *Elymus elymoides*; *Elymus multisetus*; Germination; Temperature

## 1. Introduction

The squirreltails, bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey] and big squirreltail [*Elymus multisetus* (J.G. Smith) Burtt-Davy], have a broad geographic distribution in the western United States and have been identified as high-priority species for restoration and rehabilitation of rangelands disturbed by introduced annual weeds (Clary, 1975; Arredondo et al., 1998; Jones, 1998; Clausnitzer et al., 1999; Booth et al., 2003; Jones et al., 2003; Humphrey and Schupp, 2004). Young and Evans (1977, 1982) and Young et al. (2003) noted high germinability of squirreltail seed over a wide range of thermal conditions, but did not evaluate intra-specific variability in cumulative-germination rate. Jones et al. (2003) correlated growth characteristics of three squirreltail taxa by subspecies and ecotype, but evaluated germination and emergence response for only one thermal regime. Hardegree et al. (2002) evaluated thermal-germination response of eight seedlots of *E. elymoides*,

and three seedlots of *E. multisetus*, but only estimated germination response of the median seed-subpopulation.

Germination indices are commonly used to quantify thermal response of rangeland grass and shrub species, and to assign ecological significance to differences found among and within species (Young and Evans, 1982; Jordan and Haferkamp, 1989; Romo and Eddleman, 1995). Scott et al. (1984) and Brown and Mayer (1988) reviewed several single-value germination-vigor indices and found them to confound germinability and rate elements.

Thermal-time models yield coefficients that are frequently used as indices to screen germplasm and to rank potential temperature response of species and seedlots (Covell et al., 1986; Ellis et al., 1986; Jordan and Haferkamp, 1989; Craufurd et al., 1996; Fidanza et al., 1996; Holshouser et al., 1996; Steinmaus et al., 2000; Phartyal et al., 2003; Hardegree, 2006a). Garcia-Huidobro et al. (1982a,b), Covell et al. (1986) and Ellis et al. (1986, 1987) expanded thermal-time analysis to consider the whole seed population, allowing characterization of cumulative germination response over a wide range of suboptimal and supraoptimal temperatures. Hardegree and Van Vactor (2000) suggested that a more ecologically rele-

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vant basis for evaluating thermal-germination response could be derived from predictions of cumulative-germination time under simulated conditions of field-variable temperature. Hardegee (2006a,b) and Hardegee and Winstal (2006) evaluated eight cardinal-temperature (CT), regression and statistical-gridding (SG) procedures, and concluded that the most accurate and efficient model for estimating field-variable temperature response was an SG model, which had the fewest a priori shape assumptions.

The purpose of this study was to expand upon previous evaluations of inter and intra-specific variability in thermal-germination response of bottlebrush squirreltail and big squirreltail collected from field sites in Idaho, Colorado, Arizona, Utah, and New Mexico (Jones et al., 2003). Specific objectives were: to develop a more ecologically relevant seedlot comparison based on simulated field-temperature response (Hardegee et al., 2003; Hardegee, 2006b), to evaluate this approach relative to the more common methodology of comparing CT-model coefficients (Hardegee, 2006a), and to assess previous inferences related to genetic variability in germination response (Jones et al., 2003).

## 2. Materials and methods

Eighteen seedlot-accessions of big squirreltail from Idaho, and 23 of bottlebrush squirreltail (ssp. *elymoides* and *brevifolius*) from Idaho, Utah, Arizona, New Mexico and Colorado were used in this experiment (Table 1). Initial seed procurement and subsequent nursery-seed production for 37 of the 41 accessions are described by Jones et al. (2003). The remaining accessions (T-1201, T-1207, T-1245, and T-1304) were collected and processed by USDA-ARS personnel in Logan, Utah using the same procedures described previously. Seeds used in this experiment were harvested from nursery-grown plants at the Utah State University Evans Farm, Millville, UT (41°41'39"N, 111°49'58"W) in 1997 and 1998 for germination tests in 1998 and 1999 respectively. All seedlots were tested in both years except for big squirreltail accession 1268 which did not produce sufficient seeds for inclusion in the second year of the experiment. Air-dry seeds were stored in paper envelopes at 4 °C until used in the germination experiment.

Germination response to constant-temperature was evaluated in 36 programmable environmental chambers of the type described by Hardegee and Burgess (1995). Chamber temperatures were maintained by a data-acquisition and control system that adjusted temperature up or down whenever it deviated from the programmed temperature by more than 0.5 °C. Chambers were illuminated by both incandescent and fluorescent lights which maintained a 12-h photo-period with a mean irradiance of  $16 \pm 0.4 \text{ W m}^{-2}$  during the day.

Seeds were germinated on cellulose dialysis membranes in germination cells of the type described by Hardegee and Emmerich (1992). The membranes were equilibrated with a solution reservoir of polyethylene glycol (8000) which maintained a water potential of  $-0.03 \text{ MPa}$  in the germination vial (Michel and Radcliffe, 1995). This water potential was selected to eliminate free solution on top of the membrane

without subjecting the seeds to a significant level of water stress (Hardegee and Emmerich, 1994). All seeds were dusted with Captan fungicide (wetable powder, *N*-trichloromethylthio-4-cyclohexene-1,2-dicarboximide) at the beginning of each experimental run and as needed, thereafter, to minimize fungal growth.

Germination response was evaluated at 11 constant temperatures in 3 °C increments between 3 and 33 °C. Each temperature regime was replicated in three different environmental chambers for each seedlot in each year of the experiment. Germination vials were replicated four times within each environmental chamber. Replicate vials within a chamber were randomly assigned within each of 4 blocks. Thirty seeds of each seedlot were placed in each germination vial at the beginning of each experimental run and monitored daily for germination. Seeds were counted and removed when they exhibited radicle extension of  $\geq 2 \text{ mm}$ .

Forty-one seedlots, 11 temperatures, 3 chamber replications, and 4 vial-subsamples per chamber made for a total of 5412 germination vials in each experimental year. This number could not be simultaneously accommodated among the 36 environmental chambers. All 3 and 6 °C treatments were loaded on the first day of the experiment in a given year, and the other temperature treatments were assigned a random order for germination testing. Within a given temperature treatment, seedlots were also assigned a random order for germination testing, however, all 12 germination vials for a given seedlot and temperature were always loaded on the same day. All germination data were entered into a database daily, and evaluated by treatment and seedlot for cumulative germination response. When cumulative germination response appeared to have reached a stable plateau for a period of 4–5 days, all 12 vials of a given treatment and seedlot were removed and replaced by the next seedlot in the random-priority list for that temperature. When all seedlots had been evaluated at a given temperature, the environmental chambers were reprogrammed for the next temperature-treatment in the random-priority list. Some temperature/seedlot combinations took less than a week to achieve maximum germination. The longest treatment period was 74 days for some seedlots at 3 °C.

Germination counts were pooled by seedlot within each environmental chamber, and the within-box totals were considered replicate samples for model development and analysis. Cumulative germination was calculated for every seedlot and replicated-temperature treatment for every count day of a given experimental run. Seed populations were considered to be composed of subpopulations based on relative germination rate (Garcia-Huidobro et al., 1982a). Germination data were scaled by dividing the daily-germination-percentage values by the maximum-germination percentage ( $G_{\text{max}}$ ) obtained in the optimal temperature treatment for a given accession in a given year (Covell et al., 1986). Days required to achieve 5–90% germination were calculated for each seedlot and replicated-temperature treatment by linear interpolation between daily germination percentiles from the cumulative germination curves (Covell et al., 1986). Seeds from the same accession, tested in different years, were analyzed separately.

Table 1

Collection-location information for 41 accessions of bottlebrush squirreltail (*Elymus elymoides*) and big squirreltail (*Elymus multisetus*)

Accession	Collection location	State	Latitude	Longitude	Elevation (m)
<i>E. elymoides</i> ssp. <i>brevifolius</i> (Group A)					
T-1180	NW Wagonmound	NM	36°03'16"N	104°47'41"W	2000
T-1233	Hermosa	CO	37°25'55"N	107°48'48"W	2000
T-1238	SE Durango	CO	37°12'36"N	107°14'11"W	2050
T-1239	NE Pagosa Springs	CO	37°22'33"N	106°53'57"W	2350
T-1242	N. Lake City	CO	38°13'56"N	107°15'33"W	2450
T-1245 <sup>a</sup>	NW Almont	CO	38°41'47"N	106°50'58"W	2500
T-1249	W Sargents	CO	38°23'49"N	106°28'20"W	2600
T-1260	S. Westcliffe	CO	38°06'39"N	105°27'35"W	2450
T-1264	N. Colmor	NM	36°15'54"N	104°38'31"W	1850
T-1265	N. Wagonmound	NM	36°04'11"N	104°41'23"W	1900
T-1271	SW Ocate	NM	36°06'26"N	105°06'06"W	2300
T-1272	La Cueva	NM	35°56'38"N	105°15'12"W	2200
T-1277	Tres Piedras	NM	36°38'29"N	105°58'03"W	2350
T-1299	N Flagstaff	AZ	35°20'22"N	111°33'25"W	2150
<i>E. elymoides</i> ssp. <i>brevifolius</i> (Group B)					
T-1228	Colton	UT	39°49'37"N	110°56'44"W	2150
T-1243	N. Powderhorn	CO	38°20'24"N	107°06'06"W	2750
<i>E. elymoides</i> ssp. <i>brevifolius</i> (Group C)					
T-1202	Hwy 75 X 20	ID	43°18'03"N	114°17'37"W	1350
T-1203	E. Fairfield	ID	43°20'35"N	114°41'18"W	1500
T-1205	W. Hill City	ID	43°18'58"N	115°15'26"W	1600
T-1206	E. Dixie	ID	43°19'17"N	115°20'22"W	1600
T-1304 <sup>a</sup>	Hwy 75 X 20	ID	43°18'03"N	114°17'37"W	1500
<i>E. elymoides</i> ssp. <i>elymoides</i>					
T-1175	Ditto Creek Rd.	ID	43°17'21"N	115°50'11"W	1000
T-1223	NW Carey	ID	43°20'36"N	113°51'48"W	1450
<i>E. multisetus</i>					
T-1165	SW King Hill	ID	42°58'57"N	115°15'44"W	850
T-1177	Little Ranch	ID	43°46'57"N	116°31'38"W	800
T-1178	Middle Hatley	ID	43°48'40"N	116°35'31"W	800
T-1179	Lower Hatley	ID	43°48'18"N	116°37'27"W	800
T-1182	E. Boise	ID	43°30'02"N	116°08'11"W	1000
T-1183	W. Mt. Home	ID	43°09'46"N	115°42'11"W	1000
T-1201 <sup>a</sup>	W. Dietrich	ID	42°54'06"N	114°18'50"W	1250
T-1207 <sup>a</sup>	E. Dixie	ID	43°18'35"N	115°26'14"W	1500
T-1209	Ditto Creek Rd.	ID	43°17'20"N	115°50'10"W	1000
T-1210	Ditto Creek Rd.	ID	43°21'30"N	115°49'30"W	800
T-1211	SE Mayfield	ID	43°23'53"N	115°51'39"W	1100
T-1213	NW Mayfield	ID	43°26'58"N	115°56'11"W	1100
T-1214	Black's Creek Rd.	ID	43°28'26"N	116°03'10"W	1100
T-1216	Bogus Basin Rd.	ID	43°39'51"N	116°11'26"W	1000
T-1218	Cartwright Rd.	ID	43°41'31"N	116°13'16"W	1000
T-1219	Seaman's Gulch Rd.	ID	43°42'30"N	116°15'43"W	1000
T-1220	SE Barber	ID	43°33'11"N	116°05'39"W	950
T-1268	A-line Canal	ID	43°51'44"N	116°36'08"W	950

<sup>a</sup> Not included in Jones et al. (2003).

Germination rate ( $R$ ) as a function of temperature was plotted separately for each seedlot and interpolated-subpopulation ( $G_5$ – $G_{90}$ ) and the data separated into suboptimal and supraoptimal temperature range by visual inspection (Covell et al., 1986). Linear regression was used to derive thermal-time ( $\theta$ ) and base-temperature ( $T_b$ ) coefficients for the suboptimal temperature range for individual subpopulations following the procedure described by Hardegree (2006a). A mean value of  $T_b$  was derived for each seedlot and values of  $\theta$  recalculated for each subpopulation using the common value for  $T_b$  following procedures

outlined by Hardegree (2006a) for Probit-CT and Sigmoid-CT model formulations.

Hardegree and Winstral (2006) and Hardegree (2006b) developed and tested an SG-model for predicting germination rate as a function of temperature ( $T$ ) and subpopulation-percentile ( $G$ ). The SG-model procedure, described by Hardegree and Winstral (2006), does not allow for extrapolation beyond the temperature range used in parameterization. We modified the cited procedure by extrapolating data from the 3 and 6 °C treatments to obtain a lower-temperature limit for each subpopulation. If a given

subpopulation did not germinate at 3 °C, we included a rate estimate of 0 for the temperature treatment that was 3 °C below the minimum treatment-temperature that resulted in germination.

Flerchinger and Hardegee (2004) calibrated a soil-microclimate model for predicting soil temperature and water at seeding depth at the Orchard Field Test Site in southern Ada County, ID. Hardegee et al. (2003) used this model to estimate temperature and water potential at 2-cm depth for every hour of a 38-year test period (1962–2000) on a Tindahay sandy-loam soil (sandy, mixed mesic xeric torriorthent). We used the simulated-temperature data from this previous study, and the SG-model to estimate per-day germination rate as a function of temperature for all squirreltail seedlots and subpopulations for every hour of the 38-year test period. Per-day rate estimates were divided by 24 to obtain per-hour germination-rate estimates. Per-hour germination-rate estimates represent the fractional progress toward germination for a given subpopulation during that hour (Hardegee et al., 1999). Germination time for a given subpopulation was estimated to occur when the sum of hourly, post-planting, germination rate estimates equaled 1 (Phelps and Finch-Savage, 1997; Hardegee et al., 1999, 2003). Germination time was estimated for eight planting dates (every 3 weeks) between 1 January and 28 May in all years and for all seedlots and subpopulations following the procedure described by Hardegee (2006b).

### 3. Results

Fig. 1 shows the mean, mean-maximum and mean-minimum daily temperature across all years in the test period. The year 1980 had a mean temperature during the test period that was approximately the mean of all years tested. Hourly-temperature estimates for 1980 are shown in Fig. 1 as an example of seasonal variability in diurnal-temperature amplitude. The range of mean-daily temperatures across test years for any given day was on the order of 15 °C in the month of January, rising to 18 °C for the month of May. The mean-diurnal-temperature amplitude across all years was 12 °C in January, rising to 21 °C in May.

Table 1 lists the original collection locations and elevations for all accessions. *E. elymoides* ssp. *brevifolius* was separated into three groups (A, B and C) based on morphological analysis of the parent populations as reported by Jones et al. (2003). The mean ( $\pm$ S.E.) collection elevations for the different accessions were 2225  $\pm$  64 m for *E. elymoides* ssp. *brevifolius*, group A (*brevifolius*-A), 2450  $\pm$  300 m for *E. elymoides* ssp. *brevifolius*, group B (*brevifolius*-B), 1510  $\pm$  46 m for *E. elymoides*

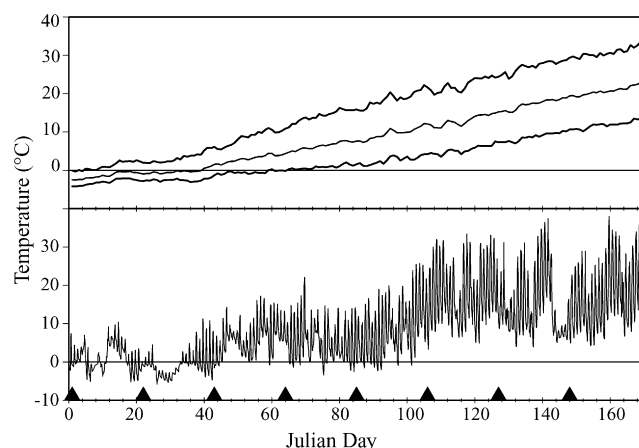


Fig. 1. Mean, mean-maximum and mean-minimum daily-soil temperature (upper graph) at 2-cm depth across all years (1962–2000), and hourly temperature (lower graph) for 1980. The mean simulated temperature in 1980 was approximately equal to the mean temperature across all years in the temperature simulation. Arrows indicate simulated planting dates.

ssp. *brevifolius* group C (*brevifolius*-C), 1225  $\pm$  225 m for *E. elymoides* ssp. *elymoides* (*elymoides*), and 1000  $\pm$  42 m for *E. multisetus* (*multisetus*). Subsequent analysis of the relationship between elevation and various germination indices showed no correlation within accession groupings.

Maximum germination percentage ( $G_{\max}$ ), days to 50% germination ( $D_{50}$ ) at 9 and 24 °C, and suboptimal thermal-time and base-temperature of the median subpopulation ( $\theta_{50}$ ,  $T_{b50}$ ) are shown in Table 2.  $G_{\max}$  represents the highest germination percentage among all treatments for a given accession and was used as the scaling factor for defining seed subpopulations  $G_5$  through  $G_{90}$ . None of these indices were correlated between measurement years within a given accession-grouping except for  $D_{50}$  of *brevifolius*-A accessions which were weakly correlated at both 9 ( $r^2 = 0.66$ ) and 24 °C ( $r^2 = 0.52$ ). Accession values for the parameters in Table 2 were averaged first across years by accession, and then a mean and standard error calculated across accession groupings.

Suboptimal  $T_b$  was negatively correlated with subpopulation for all accession groupings except *brevifolius*-C (Fig. 2). The most common suboptimal CT-models, however, require calculation of a mean value for  $T_b$  across all subpopulations (Ellis et al., 1986; Covell et al., 1986; Hardegee, 2006a). Mean values for  $T_b$  were 1.8 °C (S.E.  $\pm$  0.1) for *brevifolius*-A, 0.6 °C (S.E.  $\pm$  0.2) for *brevifolius*-B, 2.8 °C (S.E.  $\pm$  0.1) for *brevifolius*-C, 1.6 °C (S.E.  $\pm$  0.1) for *elymoides*, and 0.7 °C (S.E.  $\pm$  0.1) for *multisetus*. The suboptimal CT-model also yields values for  $\theta$  as a

Table 2  
Germination indices and thermal-time parameters for accession-groupings

Accession group	$D_{50}$ at 9 °C (days)	$D_{50}$ at 24 °C (days)	$G_{\max}$ (%)	$T_{b50}$ (°C)	$\theta_{50}$ (°day)
<i>E. elymoides</i> ssp. <i>brevifolius</i> (Group A)	11.1 (0.3)	5.1 (0.3)	95.8 (1.0)	1.7 (0.2)	79 (2)
<i>E. elymoides</i> ssp. <i>brevifolius</i> (Group B)	9.3 (0.1)a	4.1 (0.1)	93.7 (1.1)a	0.1 (0.5)	81 (6)
<i>E. elymoides</i> ssp. <i>brevifolius</i> (Group C)	9.2 (1.2)ab	3.1 (0.3)b	98.8 (0.3)	3.0 (0.8)	50 (1)
<i>E. elymoides</i> ssp. <i>elymoides</i>	9.2 (0.2)b	3.3 (0.3)	93.8 (1.1)a	1.4 (0.1)	66 (1)
<i>E. multisetus</i>	6.7 (0.2)	3.1 (0.1)b	87.4 (1.3)	0.4 (0.1)	56 (1)

Mean values within a column followed by the same letter could not be distinguished ( $\alpha = 0.05$ ). Numbers in parentheses represent 1 standard error of the mean.



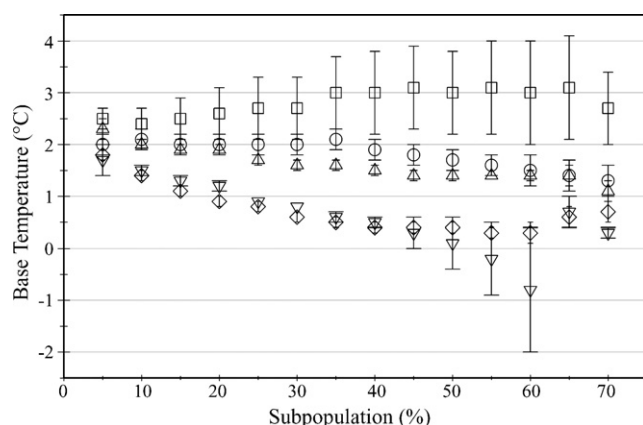


Fig. 2. Mean base temperature ( $T_b$ ) of *brevifolius*-A (circles), *brevifolius*-B (down triangles), *brevifolius*-C (squares), *elymoides* (up triangles) and *multisetus* (diamonds) accession-groupings as a function of subpopulation. Error bars represent one standard error of the mean.

function of subpopulation. Fig. 3a shows the mean and standard error of  $\theta$  as a function of subpopulation across all seedlots within the four accession-groupings. In general, *brevifolius*-C had consistently lower thermal-time requirements across all subpopulations, matched only by *multisetus* in the lower subpopulation range. Thermal-time requirements were consistently high for the other *brevifolius* accessions and intermediate for *elymoides* (Fig. 3a). Supraoptimal thermal-time was difficult to estimate from the data collected in this experiment, as germination rate was highly variable and non-linear above 24 °C (data not shown).

Fig. 3b–i show mean-cumulative germination-time estimates as a function of subpopulation for 8 planting dates between 1 January and 28 May. The 1998 and 1999 estimates for a given accession were treated as subsamples and a mean estimate of germination-time calculated. A mean-germination time and standard error were then calculated within each accession grouping as a function of subpopulation and planting date. The *multisetus* accession-grouping consistently showed more rapid germination across most subpopulations early in the season, but became relatively indistinguishable from *brevifolius*-C and *multisetus* accession-groupings later in the season (Fig. 3b–i). The *brevifolius*-A accessions were the slowest-germinating populations for all planting dates, but separation from the other accession-groupings became more apparent later in the planting season. *Brevifolius*-B accessions exhibited intermediate germination rates for every simulated planting date.

#### 4. Discussion

The simplest index for comparing seedlots is total germination percentage ( $G$ ) (Scott et al., 1984).  $G$  is the basis for the seed-testing standards published by the Association of Official Seed Analysts, and is used to establish consistency in evaluating relative seed germinability under favorable conditions of temperature and moisture (AOSA, 1996).  $G$  is also the most common germination index for comparing range-grass, seed-population response to environmental stress. Young and Evans

(1977) and Young et al. (2003) measured  $G$  for several squirreltail accessions under 55 alternating-temperature regimes to define the range and bounds of potential thermal-germination response. They found that squirreltail had high germinability over a broad temperature range but these authors did not measure germination rate, or variability in rate response within or among seed populations.  $G$  was relatively high for all seedlots tested in this experiment under favorable temperature conditions (Table 2).

Median-germination time, expressed as  $D_{50}$ , is a widely used index for evaluating germination speed (Scott et al., 1984). In the current experiment, *brevifolius*-A accessions had consistently higher values for  $D_{50}$  (slower germination) at both 9 and 24 °C (Table 2). *Multisetus* accessions had consistently lower  $D_{50}$  values in the low temperature test environment, but were similar to *elymoides* and *brevifolius*-C accessions at 24 °C (Table 2).  $D_{50}$  is often used as an index for germination rate ( $R$ ), however,  $R$  is more rigorously defined as the inverse of germination time ( $1/d$ ). Brown and Mayer (1988) describe multiple attempts to combine  $G$  and  $R$  information into single indices for assessing relative seed vigor. These combined indices usually confound any ecological or physiological comparison of seedlots as the same index-value can be obtained by few seeds germinating quickly, or many seeds germinating more slowly.

An important advance in the evolution of thermal-germination indices was the characterization and modeling of whole-population germination-response using concepts of thermal-time and cardinal temperatures (Garcia-Huidobro et al., 1982a,b). CT-models assume that thermal response is linear between a base temperature ( $T_b$ ) and an optimal temperature ( $T_o$ ), and between  $T_o$  and a maximum or ceiling temperature ( $T_m$ ). The inverse slope of rate response between these cardinal temperatures constitutes suboptimal and supraoptimal thermal-time ( $\theta_1, \theta_2$ ). Thermal-time models produce relatively powerful indices for comparing seedlots, as model coefficients integrate potential-thermal response over a relatively broad range of temperatures, and these coefficients can be distributed to describe within-population variability (Covell et al., 1986; Ellis et al., 1986, 1987). Subsequent to Gummerson (1986), modelling population-variability in germination rate has been extended to characterize the combined effects of temperature and water stress (Dahal and Bradford, 1990; Christensen et al., 1996; Cheng and Bradford, 1999; Roman et al., 1999; Shrestha et al., 1999; Meyer et al., 2000; Rowse and Finch-Savage, 2003; Bradford and Alvarado, 2005).

In the current experiment, CT-model coefficients describe a slightly different thermal-response scenario (Fig. 3a) than obtained from a simple analysis of  $D_{50}$  at two test temperatures (Table 2). *Brevifolius*-C accessions now appear to have most rapid germination (lowest  $\theta$ ), matched by *multisetus* only in the lower subpopulation range (Fig. 3a). This discrepancy can be explained by differences in  $T_b$  with *multisetus* having a mean value about 2.5 °C lower than for *brevifolius*-C for the  $G_{50}$  subpopulation (Table 2). The CT-model ignores potential variability in  $T_b$  as a function of subpopulation, which may significantly affect germination time under low-temperature field scenarios. It is also relatively difficult to assess the relative impact of  $\theta$  and

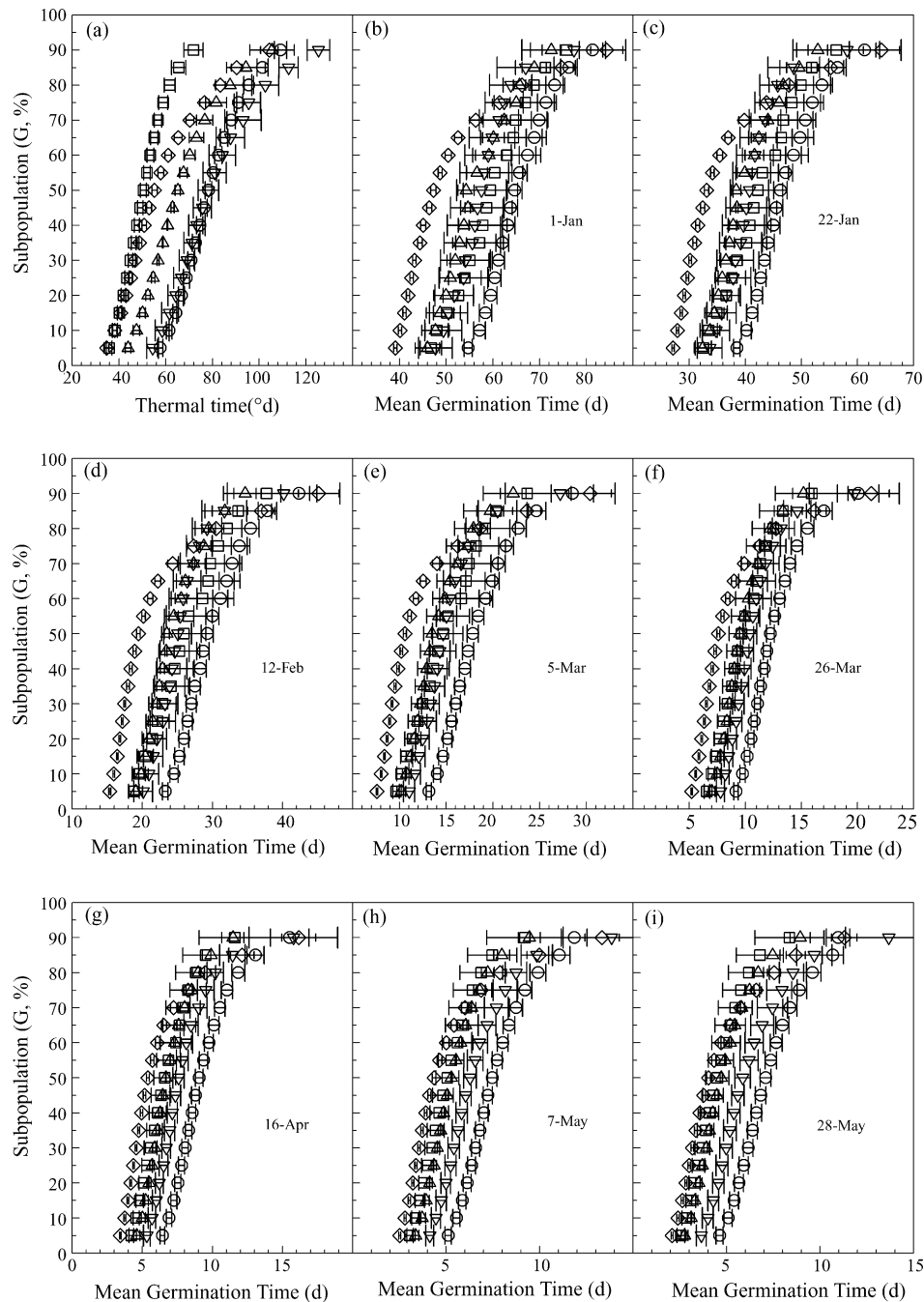


Fig. 3. Thermal-time ( $\theta$ ) distribution (a) and mean-germination time as a function of simulated planting date (b–i) for *brevifolius*-A (circles), *brevifolius*-B (down triangles), *brevifolius*-C (squares), *elymoides* (up triangles) and *multisetus* (diamonds) accession-groupings as a function of subpopulation. Error bars represent one standard error of the mean.

$T_b$  at temperatures near  $T_b$  as very small changes in germination rate in this region can translate into very large differences in germination time (Hardegee, 2006a).

Allen (2003) noted one advantage of CT-type models is that their coefficients can be linked to specific physiological processes that drive measured-thermal response. Previously developed hydrothermal and CT-type germination models, however, utilize model–shape assumptions that often require some degree of empirical adjustment to accurately predict germination time (Dahal and Bradford, 1994; Phelps and Finch-Savage,

1997; Finch-Savage et al., 1998; Kebraeb and Murdoch, 1999; Grundy et al., 2000; Alvarado and Bradford, 2002). Thermal models alone are insufficient for predicting germination and emergence in the field where seeds are subject to a number of biological, physical and chemical factors in addition to temperature variability (Hegarty, 1973; Brar et al., 1992; Finch-Savage and Phelps, 1993; Egli and TeKrony, 1996; Helms et al., 1996; Weaich et al., 1996; Hardegee and Van Vactor, 2000). Hardegee (2006b), however, showed that in the absence of other biotic and abiotic effects, thermal models can produce highly accurate

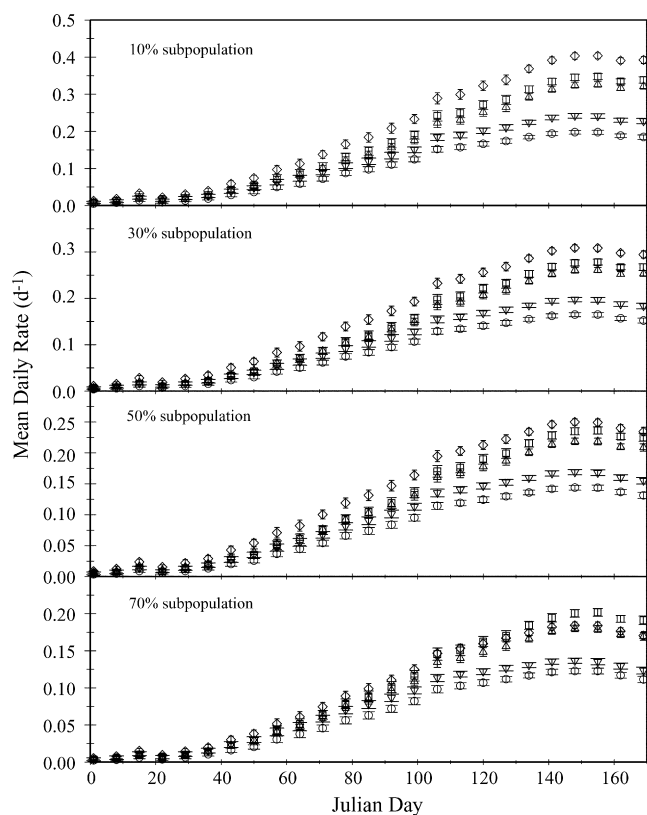


Fig. 4. Mean daily germination rate across all seedlots and all years as a function of Julian day for *brevifolius*-A (circles), *brevifolius*-B (down triangles), *brevifolius*-C (squares), *elymoides* (up triangles) and *multisetus* (diamonds) accession-groupings. Error bars represent on standard error of the mean. Only every 7th-day is shown for clarity.

predictions of germination time under field-variable temperature conditions. Hardegee and Van Vactor (2000), Hardegee et al. (2003) and Hardegee (2006b) have suggested that a more ecologically relevant basis for ranking seedlot-thermal response could be derived from model simulations of field-variable temperature response.

Fig. 3b–i demonstrates one method for seedlot comparison based on germination-time prediction that is consistent with  $D_{50}$  values estimated at 9 and 24 °C (Table 2). Early in the year, *multisetus* accessions were predicted to germinate significantly faster than all other accessions by between 5 and 15 days for subpopulations up to about 70% (Fig. 3b–e). As the simulated planting season progressed, *elymoides*, *multisetus* and *brevifolius*-C accession-groupings tended to converge to a similar pattern of cumulative germination time. *Brevifolius*-A remained the slowest accession-group, and *brevifolius*-B remained intermediate throughout the season. An alternative method for seedlot comparison is to plot daily rate sums as a function of date for different species and subpopulations (Fig. 4). The data presented in this format express the seasonal progression in relative-favorability of seedbed-thermal conditions for different seedlots and subpopulations. Hardegee et al. (2003) integrated the area under curves of this type as a single index expressing relative-germination rate as a function of seedlot and subpopulation. In addition to comparing different

seedlots, this approach could also be used to evaluate variability in seedbed microclimate among different planting years (Hardegee et al., 2003). An additional application would be to compare potential germination response of all species to modeled microclimate from each of the general collection areas. We limited our analysis to a field simulation for which we had calibrated-model data (Flerchinger and Hardegee, 2004). Uncalibrated models of the type used here are, however, relatively accurate at predicting soil temperature (Flerchinger and Hardegee, 2004).

One difference between germination indices based on CT-model coefficients, and germination assessments derived from predicted-variable-temperature response, is the effective temperature range on which they are based. CT-models and other regression-models of the type described by Hardegee (2006a,b) and Hardegee and Winstral (2006), optimize model coefficients over a broader range of conditions than is perhaps relevant in a typical field environment. For seed-collection locations in this experiment, soil moisture is typically available for germination and emergence only in the winter and early spring. The spring emergence period at the Orchard test site is generally over by mid to late May (Hardegee et al., 2003). Fig. 2 indicates that this period is generally within the suboptimal temperature range. It is, therefore, appropriate to compare these species and seedlots with CT-model coefficients for only the suboptimal temperature range. It was relatively difficult to establish supraoptimal CT-model parameters for these seedlots, as with previous studies, the thermal-response data in this range were highly variable, non-linear, and dropped off rapidly at supraoptimal temperatures (Hardegee, 2006a). Adequate characterization of supraoptimal-temperature response for CT-type models may require the more closely spaced treatment temperatures used by Hardegee (2006a) and Hardegee and Winstral (2006). It should be noted in Fig. 3 that suboptimal thermal-time estimates and germination times can only be directly compared for the first 4–5 planting dates, as some of the later planting dates included diurnal temperatures that extended into the supraoptimal-temperature range.

Jones et al. (2003) evaluated most of these same seedlots for a number of growth characteristics including germination and emergence response. Our data confirm the previous authors' conclusions that *multisetus* accessions were generally the most rapid to germinate and that *brevifolius* accessions from the Rocky Mountains (A,B) were the slowest. Jones et al. (2003) hypothesized that rapid germination of *multisetus* accessions resulted from adaptation to a warmer spring field environment. Slower germination and emergence of Rocky Mountain *brevifolius* accessions were considered an adaptation to a colder spring environment. This hypothesis seems inconsistent with the current data as *multisetus* accessions were predicted to germinate rapidly at cooler temperatures in the winter and spring. This adaptation may instead be related to a lower likelihood of frost mortality subsequent to germination in the generally warmer, lower elevation, *multisetus* environment. This warmer environment may also dry out more rapidly in the spring, favoring seedlots that can germinate at lower temperatures when moisture is still available.

## 5. Conclusions

The prediction of cumulative-germination response, under simulated conditions of field-variable temperature, provides a more robust basis for seedlot comparison than can be obtained by a simple ranking of static germination indices. Cardinal-temperature coefficients speak to a broad range of potential field conditions, but give equal weight to temperatures that may not be relevant in the field. It is also difficult to visualize the relative effect of base-temperature and thermal-time coefficients on germination-time for environments that may fluctuate around the base-temperature threshold early in the spring. Model predictions of cumulative-germination can be quantified for numerical comparisons, but are sensitive to planting date, geographic location, and other environmental factors that may affect the local seedbed thermal regime.

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